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Dioptrics of the facet lenses of male blowflies *Calliphora* and *Chrysomya*

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Summary. 1. The dioptrics of the facet lenses of two blowfly species, *Calliphora erythrocephala* and *Chrysomya megacephala*, was investigated. Measurements were performed on facet lenses ranging in diameter from 20 to 80 μm .

2. The radius of curvature of the front surface of the facet lenses, measured by microreflectometry, increases approximately linearly with the facet lens diameter.

3. The optical path difference of the facet lens and water, measured by interference microscopy, depends on the distance from the optical axis according to a parabolic function. Average refractive index values, calculated from the optical path difference profile together with estimates of the thickness profile, are between 1.40 and 1.43, with the lowest values in the largest lenses.

4. The F-number calculated from the experimental data ranges from 1.5 to 2.2. It is argued that the range of effective F-numbers is 2.1–2.4.

Key words: Fly – Facet lens – F-number – Refractive index – Interference microscopy

Introduction

A single lens, acting as an imaging device, has two main optical parameters, i.e., diameter and focal distance. In this paper we study these two parameters for the facet lenses of blowflies.

Following several predecessors, Exner (1891, 1989) established that each fly facet lens functions as a positive, inverting lens (see Seitz 1968; Wehner 1981; Nilsson 1989 for reviews with historical quotes). Only recently a series of micro-optical studies were undertaken to quantify the imaging properties of the fly facet lens in detail. Notably Kuiper (1965), considering that a single facet lens resembles a classical thick lens, estimated the

focal distance by measuring the radius of curvature of front and back surfaces, together with the refractive index. A fundamental study was performed subsequently by Seitz (1968) who showed by interference microscopy that the facet lenses consist of layers of varying thickness and different refractive indices. Subsequently, McIntyre and Kirschfeld (1982), in the course of a study on the effect of chromatic aberration on image quality (which effect actually appears to be insignificant), determined the average refractive index at the axis and at the edge of the lens, as well as its dispersion.

Here we present measurements on facet lenses over a wide range of diameter values. We determined the radius of curvature of the front surface as well as the optical path profile as a function of the distance from the axis. From these two measurements it is possible to calculate the optical quality of the fly facet lens quite straightforwardly.

We have selected for this analysis two blowfly species of which the males are known to have a wide variation in facet sizes within one and the same eye, i.e., *Calliphora erythrocephala* (Kuiper and Leutscher-Hazelhoff 1965; Stavenga 1979) and *Chrysomya megacephala* (van Hateren et al. 1989). The latter species, as acknowledged by its species name, is particularly ideal in this respect, because the male has huge facets dorsally, whilst ventrally the facet sizes are quite ordinary.

Materials and methods

Flies. Corneal facet lenses of male blowflies *Calliphora erythrocephala* and *Chrysomya megacephala* were investigated; radius of curvature of the front surface, optical path profile, diameter, and thickness were measured by the following optical methods.

Microreflectometry. Live flies were mounted in a half-sphere holder which could be rotated on the stage of a Zeiss photomicroscope equipped with a bright field epi-illuminator, thus allowing measurements of facet lenses from various areas of the eye. The radius of the front surface of the facet lenses was determined with a micro-

reflectometrical method (Stavenga and Leertouwer 1989). Briefly, in the epi-illumination microscope an annulus pattern (Fig. 1a–c), consisting of 6 equidistant rings and a cross, is imaged by the front surface, acting as a spherical mirror (Fig. 1b). From the magnification, m , and the distance between object and image pattern, c (which is determined by using a flat mirror), the radius of curvature, r_o , is derived: $r_o = 2\text{ cm}/(1 - m^2)$. The magnification was measured by scanning the image plane of the microscope with a pinhole, imaged at a photomultiplier. Pinhole and photomultiplier were mechanically coupled, so during scanning they moved together. The diameter of the facet lens, taken as the diameter of the largest inscribed circle, was determined by scanning the image plane of the microscope with the facet in focus (Fig. 1c). The experimental error in the measurements was approximately 2%.

Interference microscopy. Isolated corneas were obtained by slicing a section of the eye with a razor blade vibratome (Kirschfeld 1967). By gently brushing the debris from the remaining corneal dome, clear corneal facet lenses resulted fairly easily. Small sections were cut and selected for Jamin-Lebedeff-interference microscopy, with an accordingly modified Zeiss photomicroscope. These parts were immersed in demineralized water in a closed chamber, thus preventing rapid dessication and allowing measurements over several hours during which deterioration proved negligible. (In the initial measurements we used as the immersion fluid a Ringer's solution, but the almost unavoidable evaporation resulted in unwanted modification of the salt concentration.) We could not observe a change in the shape or structure of the isolated corneas when immersed in water during the experimental period.

In the interference microscope a polarized incoming beam is split into 2 perpendicularly polarized beams. One beam then travels through the object to be investigated and the other through a reference medium. Subsequently, the beams are joined again and thus interfere. Finally, after passing a fixed Sénarmont compensator and a rotatable analyzer the resulting interference pattern is observed, photographed (Fig. 4b, c), or quantitatively analyzed with the scanning photomultiplier system.

The two beams interfere destructively, i.e., result in a black part of the photograph, when the corresponding difference in optical path equals $(h + \alpha/180^\circ)\lambda$, with h an integer, α the angular position of the analyzer, and λ the wavelength of the light; the value of h is determined with an Ehringhaus quartz compensator. We used the green mercury line with wavelength 546 nm. The refractive index of the water was $n_w = 1.334$.

Fluorescence microscopy. The optical path is the product of refractive index and geometrical path, and thus, if we want to know both parameters, we must measure one of them in addition to the optical path. We measured the geometrical path by cutting small pieces of cornea (see Fig. 4) and sticking such a piece on its side in a film of vaseline. Subsequently we photographed side-on views by making use of the autofluorescence of the facet lenses. Good results were obtained with blue-induced green fluorescence. However, a procedure in which first the cornea was soaked in a solution of fluorescein yielded better, more contrastful photographs of the thickness profile of the facet lenses (Fig. 8). No apparent change in shape due to fluorescein uptake could be noticed. From the photographs the thickness, t , can be estimated. Together with the optical path difference on axis, δ_o , the average refractive index of the facet lens on the axis, n_1 , follows from $n_1 = n_w + \delta_o/t$. We note that the photographs also allowed the estimation of other geometrical parameters, including the radii of curvature of front and back lens surfaces, diameter, and thickness profile. The relation between the radius of the front curvature and the diameter appeared to be in agreement with that found with the optical methods described above, but because the experimental errors in the data obtained from the fluorescence photographs were about 10%, and the procedure was laborious, no attempt was made at a systematic survey.

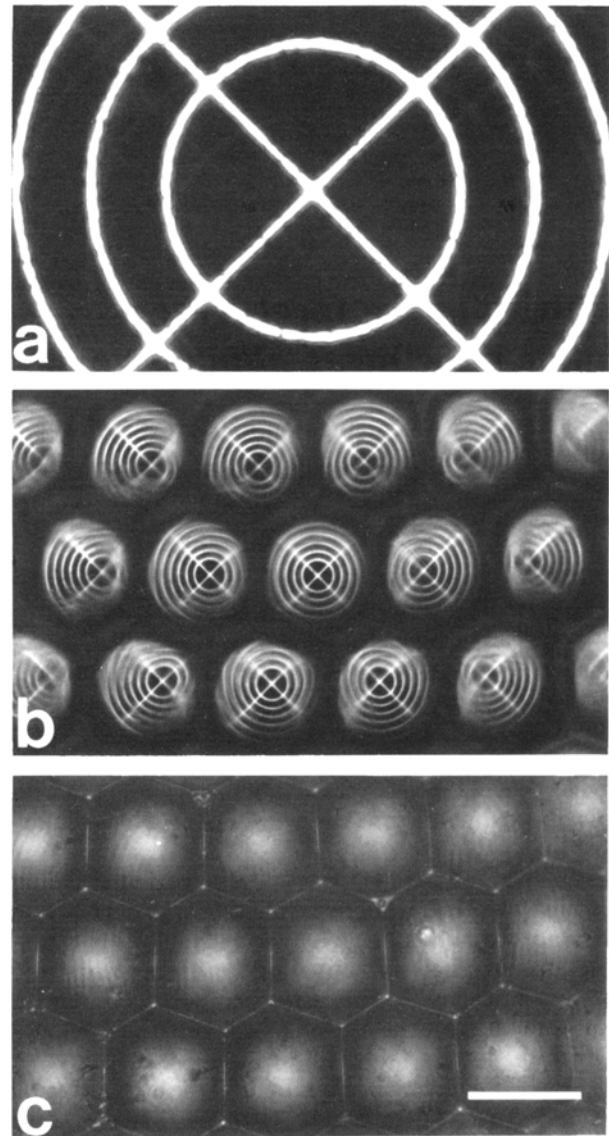


Fig. 1. **a** Annulus pattern used in the microreflectometrical estimation of the radius of curvature of the facet lens front surface; the pattern is imaged by a flat mirror. **b** The pattern imaged by an array of facet lenses (*Chrysomya*). **c** The same array but with the boundary of the facets in focus for determining the diameter. Scale bar = 25 μm

Results

Radius of curvature of the facet lens front surface

The radius of curvature of the front surface of the facet lenses was determined with a microreflectometrical method on live flies. An annulus pattern (Fig. 1a) was imaged by the array of facet lenses (Fig. 1b). The mirrored annuli are almost perfectly spherical up to the boundary of the facet lenses, thus proving that the facet lenses have very approximately an ideal, rotationally symmetrical front surface. From the magnification, m , and the distance between object and image, c , the radius of curvature was calculated: $r_o = 2\text{ cm}/(1 - m^2)$. Calcula-

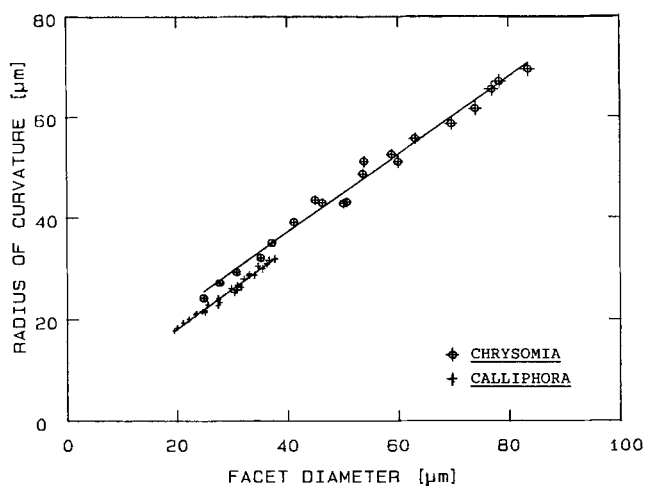


Fig. 2. Radius of curvature of the front surface r_o of facet lenses of male blowflies, *Calliphora erythrocephala* and *Chrysomya megacephala*, as a function of facet diameter

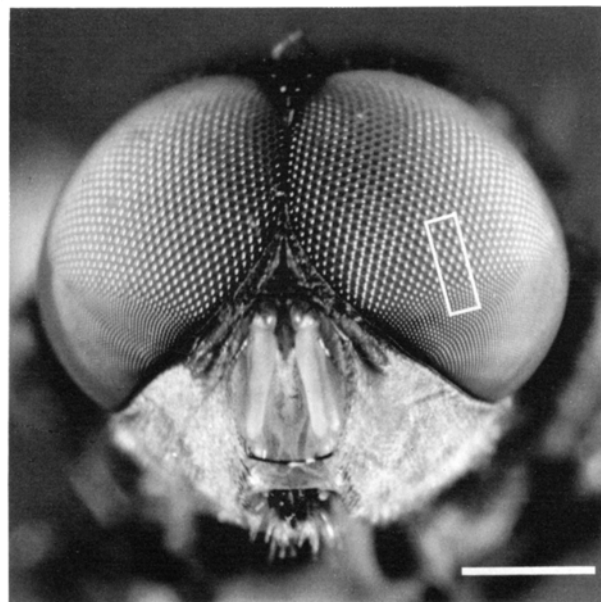


Fig. 3. Head of a male *Chrysomya megacephala*. Dorsally the facets are much larger than ventrally. Scale bar = 1 mm

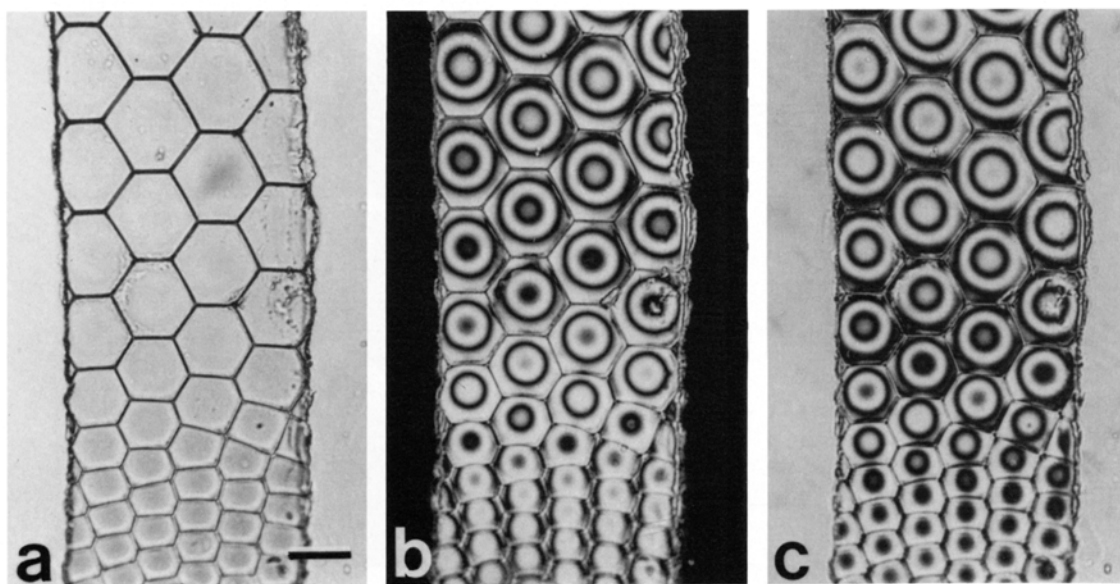


Fig. 4. **a** A section from the equatorial region of a male *Chrysomya* eye (indicated in Fig. 3). **b**, **c** Jamin-Lebedeff interference microscopy from the section of **a** under different angular settings of the analyzer. The rotational symmetry of the optical path difference is apparent. Scale bar = 50 μm

tions were performed for the two inner annuli. The r_o values resulting from these two calculations never differed more than the experimental error. Hence, the front surface can be considered to be spherical. However, the value of r_o appears to depend distinctly on the facet lens diameter as is demonstrated in Fig. 2. It appears that for both blowfly species, *Calliphora* and *Chryso-*

myia, the relationship between radius of curvature r_o and diameter D is quite linear; for *Calliphora* $r_o = 0.78D + 2.6$ and for *Chrysomya* $r_o = 0.77D + 6.5$, with both r_o and D in μm .

Optical path and refractive index

The optical path difference of the facet lenses and water was determined by Jamin-Lebedeff interference microscopy. As an example a small section of the cornea of the male *Chrysomya* (Fig. 3) is shown immersed in water (Fig. 4a-c). The section was taken from an equatorial region, where there is an abrupt change in facet

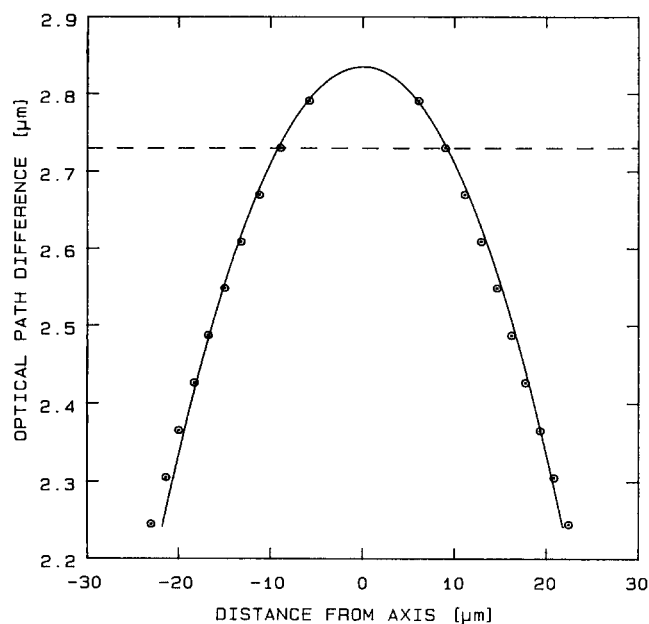


Fig. 5. Profile of the optical path difference between a facet lens (of *Chrysomyia*) and the immersion fluid, demineralized water. Dotted line indicates a path difference of 5λ , as determined by a quartz compensator

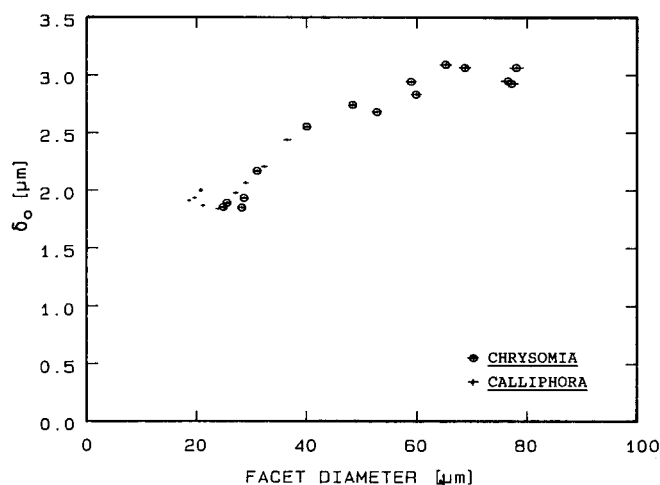


Fig. 6. The optical path difference on axis δ_0 as a function of facet lens diameter

size (Fig. 3; see also van Hateren et al. 1989). The dark interference rings (Fig. 4b, c) approximate well a perfect circle, and we thus can conclude that also in the case of the optical path the lenses exhibit rotational symmetry.

Scanning the interference patterns through the center under different settings of the analyzer yields the positions of the dark rings and hence the corresponding optical path difference. The resulting profile of the optical path difference (Fig. 5) can be approximated well by a parabolic function $\delta(x) = \delta_0 - x^2/2r_p$, where δ_0 is the value of the optical path difference on the axis and r_p

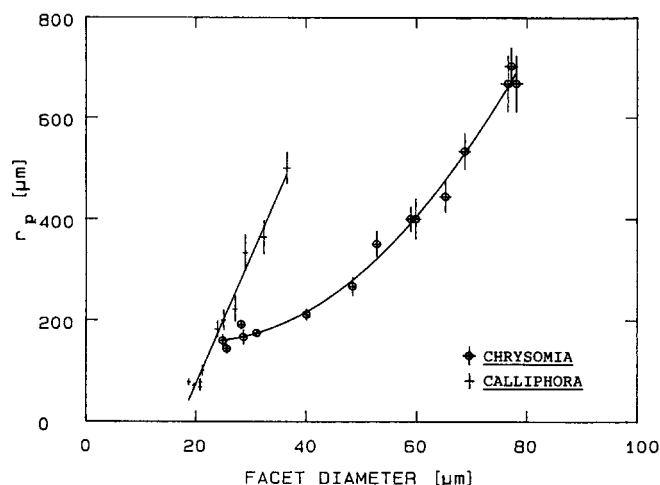


Fig. 7. The parabola parameter r_p as a function of lens diameter

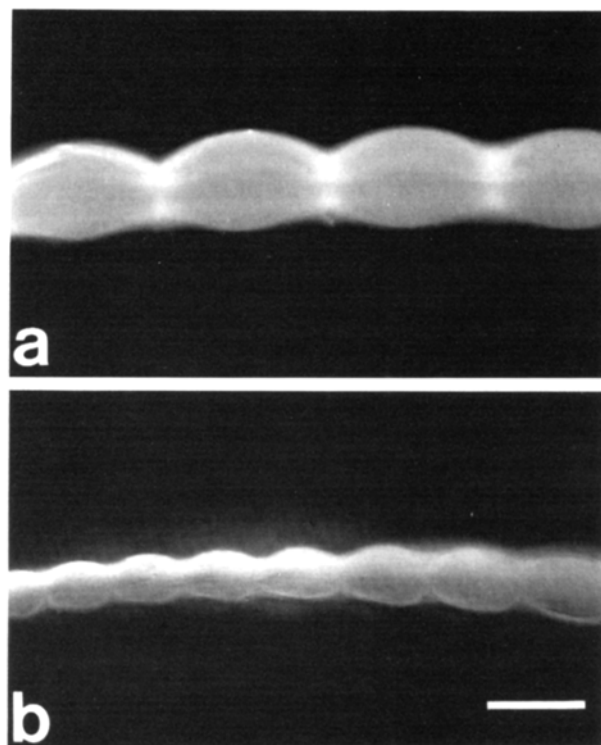


Fig. 8. Side-on view of corneal sections (*Chrysomyia*); **a** dorsal region, **b** equatorial region. Scale bar = 50 μm

the radius of curvature of the parabola in the apex. The estimated values of δ_0 and r_p , as a function of facet lens diameter, are presented in Figs. 6 and 7, respectively. The data for δ_0 obtained from *Calliphora* and *Chrysomyia* are virtually indistinguishable. However, the values for r_p differ.

Before we discuss whether the latter deviation between both species has great significance, we will first shortly elaborate on the optical path data by bringing in estimates of the thickness of the facet lenses. Their cross-section was visualized by soaking corneal sections, such as those of Fig. 4, in fluorescein and photographing

the blue-induced green fluorescence side-on. Figure 8 shows typical results. The lenses generally appear to be biconvex. The geometrical thickness t together with the optical path δ_0 , which was read from Fig. 6 by using the value of the facet lens diameter, yield the average refractive index on axis $n_1 = n_w + \delta_0/t$, using $n_w = 1.334$. Figure 9 presents the estimates for a number of different-sized facet lenses and indicates that the refractive index on axis decreases with increasing diameter.

Focal distance and F-number

In the optical path difference measurements the medium on both sides of the facet lenses was demineralized water with refractive index $n_w = 1.334$. In the normal situation the refractive index of the object space of the facet lens is 1, and that of the image space 1.337 (Seitz 1968), virtually identical to n_w . Immersing the facet lens in water with refractive index n_w has the same effect as adding a contact lens with power $(n_w - 1)/r_o$. In the thin lens approximation, the power of the facet lens can then be calculated from $P = (n_w - 1)/r_o + 1/r_p$. Hence, the focal distance (in air), $f = 1/P$, can be directly calculated from the data of r_o (Fig. 2) and r_p (Fig. 7). Figure 10a, presenting the results, shows that for both blowfly species the focal distance of the facet lenses increases linearly with their diameter. Note that the contribution to P from the first term is dominant with respect to that from the second term.

An alternative way for estimating the focal distance is offered by the thick lens formula $P = P_o + P_i - tP_oP_i/n_1$, where $P_o = (n_1 - 1)/r_o$ and $P_i = (n_w - n_1)/r_i$, with r_i the radius of curvature of the back surface of the facet lens. From photographs like those in Fig. 8 the values of r_o , r_i , and t can be estimated, of course. Together with the values of n_1 and n_w , the power P and the focal distance f then readily follow. However, the accuracy is less than that of the previous method, and furthermore the lens is assumed to be homogeneous, which is not valid (e.g., Seitz 1968). It nevertheless appears that the resulting values do not differ significantly from each other. Yet it emerges simultaneously that the effect of the thickness on the power through the third term in the thick lens formula is of the order of a few percent, and hence the thin lens approximation appears to be quite acceptable. Because $r_o \lesssim -r_i$ and $(n_1 - 1)/(n_w - n_1) \approx -5$, we note that P_o is larger than P_i by a factor $\gtrsim 3$, or the power of the front surface mainly determines the power of the facet lens.

The value of the F-number, calculated with $F = f/D$, appears to vary hardly in the investigated diameter range: it scatters around 2.0, except for the smallest lenses of *Calliphora* (Fig. 10b). The small diameter lenses were cut from the most ventral part of the cornea. Since Exner (1891, 1899), it is well-known that in compound eyes the optical axis of the dioptric system can strongly deviate from the visual axis of the ommatidium (and its photoreceptor cells), especially at the eye periphery (see Stavenga 1979). We therefore estimated the angle

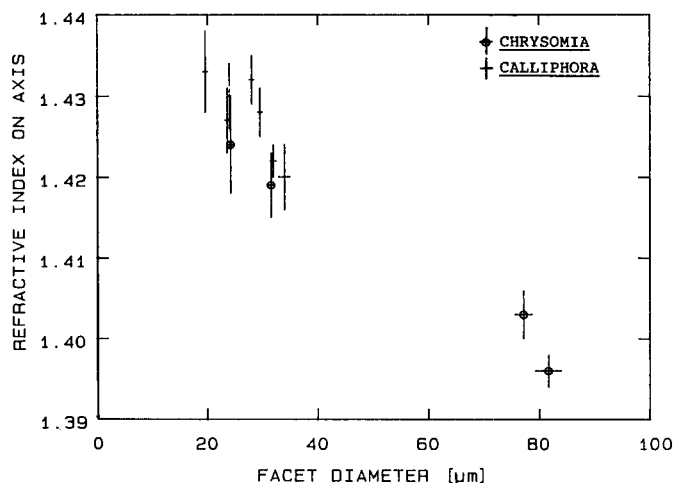
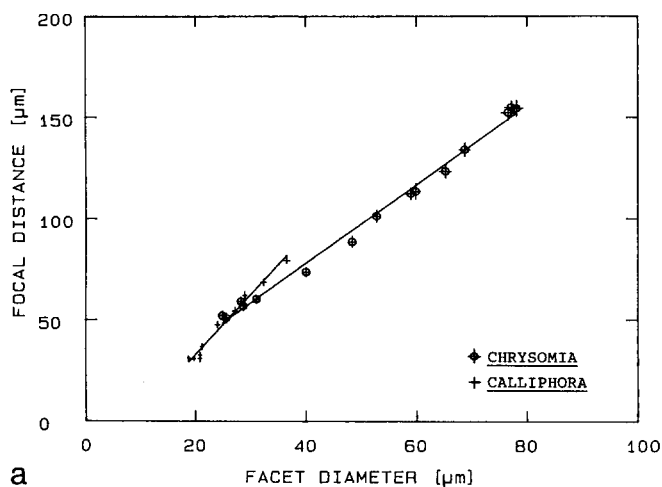
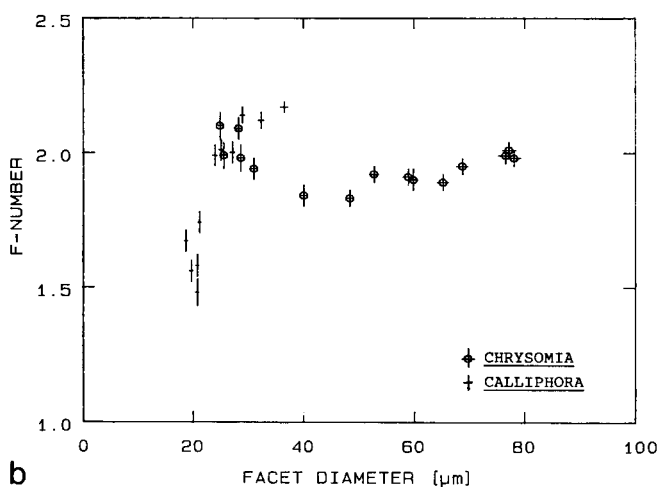


Fig. 9. Average refractive index on axis calculated from the optical path difference on axis and the thickness estimated from photographs as in Fig. 8



a



b

Fig. 10. Focal distance (a) and F-number (b) as a function of facet lens diameter

between these axes by observing the pseudopupil and the corneal reflection with a low aperture objective. It readily appeared that most ventrally in *Calliphora* the optical and visual axes deviate from each other by well

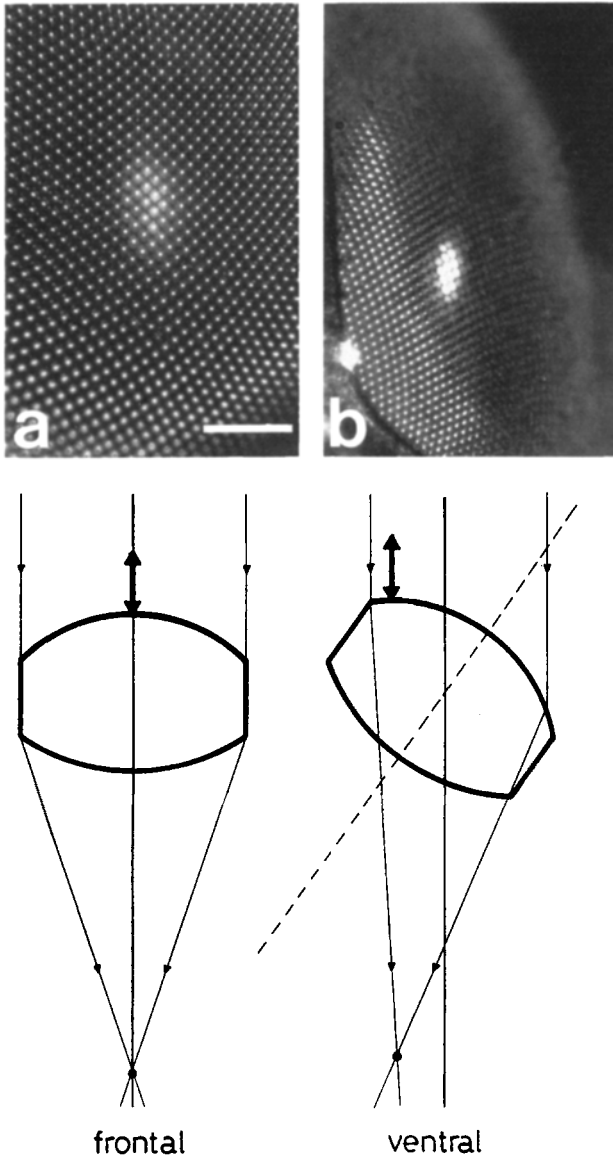


Fig. 11a, b. Epi-illumination of the eye of a *Calliphora*. **a** In the ideal case, found in the frontal part of a fly eye, the optical axis coincides with the ommatidial, visual axis. Then the reflecting pseudopupil, due to the activated pupil mechanism, is centrally located in the area of corneal facet reflections. **b** In the most ventral region of the eye, the corneal pseudopupil is strongly displaced from the corneal reflections, thus demonstrating the large angle between the visual and optical axis (dashed line in diagram). In the ventral region the angular separation between the visual and optical axes can go up to well over 35°, and thus the effective area of the facet lens is strongly reduced. Scale bar = 200 μm

over 35°, so that the lens opening is effectively reduced by 20% or more (Fig. 11). Furthermore, because the lens has thickness and is ventrally positioned quite obliquely to the incoming light beam, part of the light entering the lens through the front surface will leave the lens sideways, before reaching the back surface. Therefore, although the F-number of the ventral lenses for axial light is 1.5–1.7, we estimate that the corrected F-number will be substantially larger, i.e., around 2.0.

In the equatorial region of *Chrysomya* the same phenomenon is observed, i.e., there the optical axes are distinctly oblique with respect to the visual axes. From pseudopupil measurements we estimate that the deviations are of the order of 16°, or from the calculated F-numbers in the equatorial region, $F \approx 1.8$ (lens diameters 40–60 μm , Fig. 10b), we derive that the actual F-numbers will be ≈ 1.9 .

Discussion

Radius of curvature

The facet lenses of the two blowfly species examined here exhibit an approximately linear relationship between the radius of curvature of the front surface r_o and diameter D : the data can be roughly described by $r_o = 0.85 D$ over a diameter range from 20 to 80 μm . This relationship appears to hold approximately for dipteran flies in general (Stavenga and Leertouwer 1989).

Optical path and refractive index

Fly facet lenses appear to behave as ideal, diffraction-limited lenses (Stavenga and van Hateren, unpublished). An incoming plane wave emerging from a distant point source is converted by the lens into part of a spherical wave centered at the focal point (van Hateren 1989). As is common in paraxial optics, the spherical wave in an axial plane is described by a parabolic function: $x^2/2f$. Similarly, the action of the water contact lens, added to the facet lens upon immersion, on the incident wave is described by a parabolic function: $(n_w - 1)x^2/2r_o$. It therefore may not be completely fortuitous that the optical path difference profile of a fly facet lens immersed in water is also described by a parabolic function: $\delta_o - x^2/2r_p$.

The values for the axial path difference, together with those for the geometrical thickness, yielded a quite distinct dependence of the average refractive index on axis on the lens diameter. The value for the smaller facets (*Calliphora*) is about 1.430, slightly less than the value 1.444 calculated by Seitz (1968). McIntyre and Kirschfeld (1982) measured for 2 facet lenses of the housefly *Musca* 1.445 ± 0.003 and 1.434 ± 0.003 . The refractive index value of the largest facets (of *Chrysomya*) is about 1.400.

We presume that this size dependence is related to how the facet lenses grow. The lens material is deposited gradually, from the proximal side, by the primary pigment cells (Goldsmith and Bernard 1974). Friza (1928) concluded that dipteran corneal facet lenses have a highly refractile layer near the front surface. Furthermore, from his interference microscope studies on thin sections, Seitz (1968) derived that the facet lens consists of layers with refractive indices decreasing drastically from distal towards proximal, i.e., from 1.473 through 1.453 to 1.415. An even more refined picture is provided

by Lohrer (1979), who studied the optics of corneal facet lenses of the blackfly, *Bibio marci*. Specifically in the large facets of male bibionids the refractive index can drop sharply from over 1.50 distally to 1.35 proximally. Apparently the refractive index of the deposited material, or its density, decreases during the growth process. It seems that this decrease is progressive in the larger lenses. As we have found, most of the power of the lenses is determined by the front surface, because of the large refractive index difference between air and the lens. This effect is enhanced by the fact that the material with the highest refractive index is concentrated near the front surface of the facet lens. In other words, the facet lens can indeed be considered to approximate a thin lens.

From the fluorescence photographs the geometrical thickness profile could be determined. From these data, together with those for the optical path difference profile, the refractive index profile could be calculated. As a rule, at most only a slight refractive index increase from center to edge was found (see Vogt 1974 on *Musca*).

Focal distance and F-number

The focal distance of the blowfly facet lens was calculated from optical measurements of the frontal radius of curvature and the optical path profile, and the F-number then followed by dividing by the diameter. We concluded that, after correction for skewness, the range of actual F-numbers is 1.9–2.2. However, in intact fly eyes the primary pigment cells of an ommatidium act as a diaphragm, and hence the effective F-number will be slightly larger than the F-number determined for a facet lens in an isolated cornea. If the effective diameter is about 0.9 times that of the real diameter (see Stavenga 1979; van Hateren, pers. comm.) the range of effective F-numbers for the two blowfly species becomes 2.1–2.4.

Previously, Stavenga (1975) derived from pseudopupil measurements $F=1.9$ for the housefly *Musca*, and van Hateren (1984) produced F-number values between 2.0 and 2.5 from measurements of photoreceptor angular sensitivities via rhabdomere radiation patterns in *Calliphora*. Van Hateren (1985), furthermore, calculated with a wave-optical model for the facet lens – rhabdomere system that the on-axis efficiency of the photoreceptors is about optimal in the above F-number range, but that on-axis sensitivity is achieved at somewhat lower values.

We have to remark, however, that the optimal value of the F-number of a facet lens in a real eye may depend on other factors than those involved in the van Hateren (1985) model. For instance, with skew facet lenses focusing will no longer be ideal, i.e., free from aberrations (Fig. 11b). Furthermore, the characteristics of the rhabdomeres are quite variable, e.g., the rhabdomeres in the dorsal eye of the male *Chrysomya* strongly taper and are twice as large as those in its ventral eye and in *Calliphora* (van Hateren et al. 1989), and the distance between the rhabdomeres may vary over the eye (van Hateren, pers. comm.). Nevertheless, the present data rein-

force the conception that F-numbers of about 2.0–2.5 are optimal for fly vision.

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